# Abundance, Substrate Angle, and Desiccation Resistance in Two Sympatric Species of Limpets

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(2 Text figures)

## INTRODUCTION

Two COMMON LIMPETS, *Collisella digitalis* (Eschscholtz, 1883) and *C. scabra* (Gould, 1846) have overlapping distributions in the upper intertidal spray zone on rocky shores of the Northwest Pacific coast of North America. HAVEN (1971) found that *C. digitalis* is more abundant on vertical surfaces, while *C. scabra* dominates horizontal surfaces. He assumed this preference to be due to differential abilities to withstand desiccation which presumably varies with rock angle and perhaps the angle of incident light. However, a variety of factors can affect rates of desiccation, including temperature, ambient humidity, and wind velocity (WOLCOTT, 1973) as well as color, roughness, orientation of substrate and wave exposure. In this study I report field work demonstrating a high correlation between the abundance of *C. digitalis* and *C. scabra* and rock angle, and the results of laboratory measurements of angle of substrate and desiccation resistance of small and large members of the two species. The relationship between size and angle in the field is also discussed.

It has been argued that one of the chief limiting factors affecting distributions of rocky intertidal biota is desiccation. There is, however, little evidence for this (DAVIES, 1969) and it remains to be demonstrated that physical conditions exceed physiological tolerances of the biota such that they are limiting (WOLCOTT, *op. cit.*). Extensive experimental evidence shows that population characteristics and abundances of intertidal organisms are strongly influenced by biological interactions (CONNELL, 1972; DAYTON, 1971, 1975; PAINE, 1969). The significance of the results of this study is discussed with respect to allocation of space and food resources in competition between these two species of limpets.

## ANGLE OF SUBSTRATE AND ABUNDANCE

The relationship between the angle of slope of the substrate and the abundance of *Collisella digitalis* and *C. scabra* was measured on 17 intertidal rock habitats in Zone 1 (RICKETTS & CALVIN, 1968) in a locality at Dillon Beach, California, U.S.A. Each rock was partitioned into quadrats using a 0.25 m² grid. Grid corners were marked with paint at each sampling time. The entire surface of each rock was covered with as many quadrats as would fit. The angle of each quadrat was measured to the nearest degree using a Brunton pocket transit attached to a board placed flat on each quadrat. Every limpet on each quadrat was measured and counted *in situ*. Limpet lengths were measured to the nearest 0.5 mm with vernier calipers. Counts and measurements were made at 4 to 6 week intervals from April 1974 to May 1975.

A significant relationship between abundance and angle was found when the logarithm of

$$\text{number of limpets per } 0.25^2 + 1$$

was plotted against angle at 5° increments for *C. digitalis* and *C. scabra* (Figure 1). Abundance declines linearly with angle for *C. scabra* while abundance increases linearly with angle for *C. digitalis*. These results support HAVEN's (1971) findings that the abundances of *C. scabra* and *C. digitalis* vary on horizontal, intermediate, and vertical slopes. Haven, however, did not examine the relationship between abundance and angle for the 2 species at 5° degree angle increments. The results in Figure 1 are representative of the entire sampling period.

## ANGLE OF SUBSTRATE AND SIZE

Field measurements of the relationship of average length (mm) and angle are shown for *Collisella digitalis* and *C. scabra* in Figure 2. The results shown are mean lengths from size frequency distributions pooled over rocks and
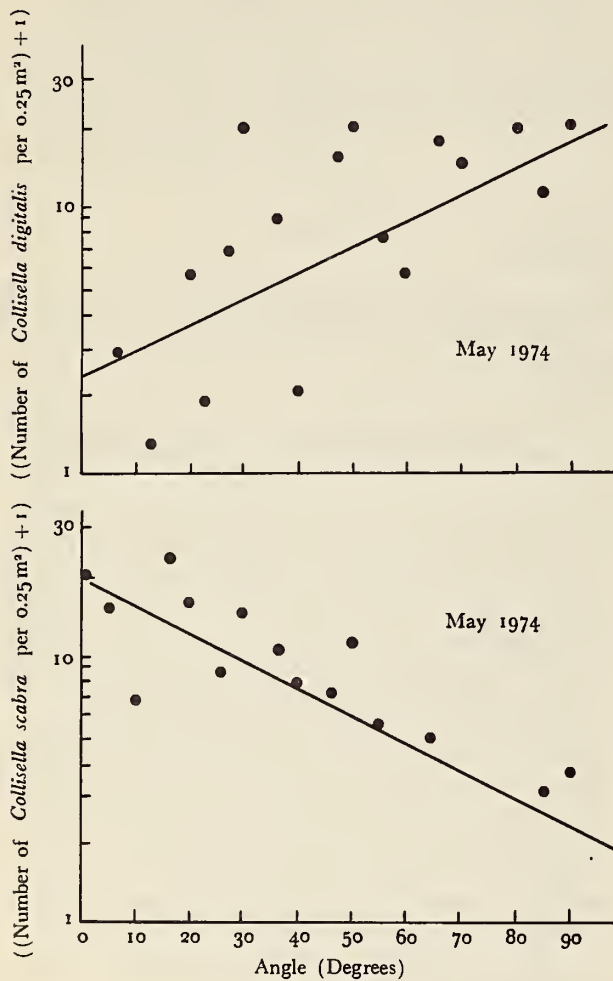
Figure 1

Relationship of abundance of *Collisella digitalis* and *Collisella scabra* to angle of substrate. Abundance is expressed in terms of ((numbers of limpets per 0.25 m²) + 1). The following equations are regressions fitted to abundance and angle data:

*Collisella scabra*
$$Y = -0.01X + 1.30 \qquad r = -0.79 \qquad p < 0.001$$
*Collisella digitalis*
$$Y = 0.01X + 0.36 \qquad r = 0.74 \qquad p < 0.001$$
Regressions are in the form $Y = a + bX$ where $Y = \log (Y + 1)$, $a = \log A$, $b = \log B$
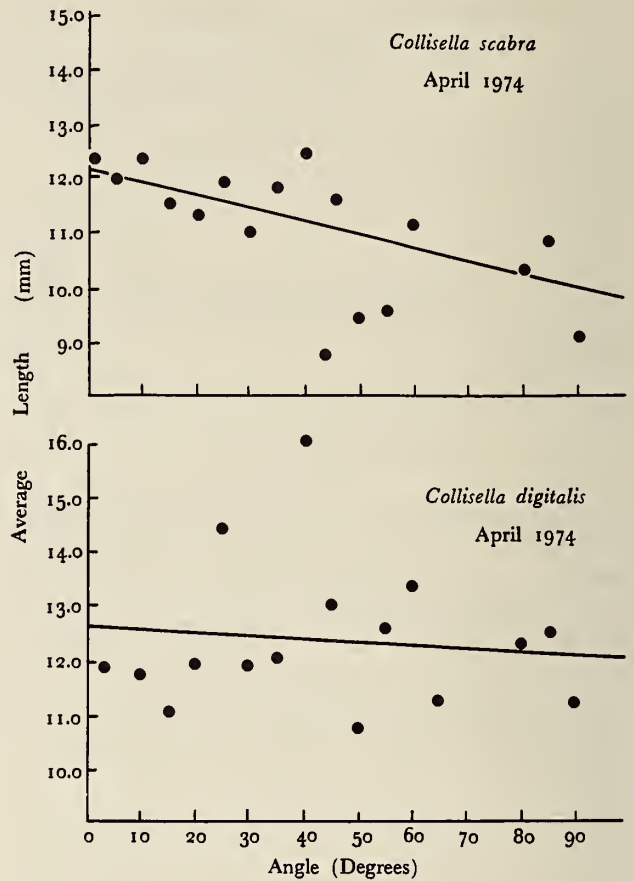


Figure 2

Relationship of average length (mm) of *Collisella scabra* and *Collisella digitalis* to angle of substrate. The following equations are regressions fitted to length and angle data:

*Collisella scabra*
$$Y = 12.2 + -0.026X \qquad r = -0.69 \qquad 0.01 > p > 0.001$$
*Collisella digitalis*
$$Y = 12.5 + -0.004X \qquad r = -0.07 \qquad 0.50 < p < 0.90$$

There is no significant relationship between length of *C. digitalis* and angle of substrate. These results do not agree with HAVEN (1971) who found *C. digitalis* largest on vertical surfaces.

## ANGLE OF SUBSTRATE AND RATES OF DESICCATION

The relationship between resistance to desiccation and angle of the substrate of *Collisella digitalis* and *C. scabra*

quadrats at 5° angle increments. Figure 2 is typical for 10 of the 11 study months. There is a significant relationship between length of *C. scabra* and angle of substrate in the field. Average length declines linearly with angle.

was studied in experiments in which weight losses of limpets of different size placed on surfaces differing in angle in a desiccator were measured. These experiments test only the effect of an angle on desiccation. It is believed that the angle at which a limpet sits could affect the rate at which water escapes by passing between the shell and substrate.

Limpets were collected from vertical rock surfaces. A few animals were captured from variable rock surfaces due to the absence of large *Collisella scabra* on vertical rocks. Only whole animals with intact shells were used in the experiment. The experimental animals were taken directly from the field or the water table (if kept overnight), placed in a plastic container with sea water and left to acclimatize for 15 minutes. Limpet length was measured to the nearest 0.5 mm with vernier calipers. The size distributions of the limpets of both species used in the experiment were identical.

Limpets were placed on microscope slides, set in small plastic dishes. Excess sea water from the shell was wiped off before the limpet was placed on the slide. The slides were oriented in 3 positions: 0° (horizontal), 45° (intermediate), and 90° (vertical). All limpets were initially oriented upwards on the 45° and 90° angle surfaces. Limpets were dried in a glass desiccator with dried calcium chloride serving as a desiccant. Weighings were made on a Mettler balance every hour for 5 hours. Humidities were measured with an Airguide Relative Humidity Indicator inserted into the desiccator. Humidity readings were made before the chamber was opened and after it was closed again during weighings. Relative humidity varied from 5% to 48% in the experiments. Records of room humidity, made by a sling psychrometer, varied from 57% to 74%. At the end of the experiment, the limpets were taken to the aquaria in the water table and immersed in sea water to dislodge them from the microscope slides. Any dead limpets were recorded.

Percent weight loss after 5 hours was calculated for each limpet as follows:

$$\% \; wt_5 = \frac{wt_1 - wt_5}{wt_1} \quad \text{where}$$

$\% \; wt_5$ = percent weight loss after 5 hours of drying
  $wt_1$ = initial weight (g) of limpet
  $wt_5$ = weight (g) of limpet after 5 hours in desiccator

Three way analysis of variance was used to test % weight loss after 5 hours drying between species, angle and length of limpet (Table 1). The 2 size classes used were limpets between 7.0 and 10.0 mm and limpets between 12.5 and 15.5 mm. There is a significant difference of % weight loss after 5 hours between angle $(0.05 > p > 0.025)$. There is no significant difference in drying rate between

### Table 1

Summary of calculations of analysis of variance for desiccation experiments testing percentage weight loss after 5 hours of small and large *Collisella digitalis* and *Collisella scabra* at three different angles of slope.

| Source of Variation | Degrees of freedom | Mean Square | F |
|---|---|---|---|
| Main Effects | | | |
|   A Angle | 2 | 0.0046 | 3.833 [1] |
|   B Species | 1 | 0.0006 | 0.500 ns |
|   C Size | 1 | 0.0237 | 19.750 [2] |
| First Order Interaction | | | |
|   A × B | | | |
|   (Angle × Species) | 2 | 0.0011 | 0.917 ns |
|   A × C | | | |
|   Angle × Size) | 2 | 0.0031 | 2.583 ns |
|   B × C | | | |
|   (Species × Size) | 1 | 0 | 0 ns |
| Second Order Interaction | | | |
|   A × B × C | | | |
|   (Angle × Species × Size) | 2 | 0.0024 | 2.00 ns |
| Error within subgroups | 48 | 0.0012 | |

[1] $0.05 > p > 0.025$ significant
[2] $p < 0.001$ highly significant
ns not significant

species $(0.50 > p > 0.25)$. There is a highly significant difference in desiccation rate between the 2 size classes tested $(p < 0.001)$. First order interactions (between angle and species; between angle and size; and between species and size) are not significant $(0.50 > p > 0.25; \; 0.10 > p > 0.05; \; p > 0.75)$. There is no significant second order interaction (between angle, species and size) $(0.25 > p > 0.10)$.

Relationships between limpet size and weight loss are summarized in Table 2 for limpets between 7.0 and 17.0 mm. Results show that there is a negative correlation between % weight loss after 5 hours and length of limpet for *Collisella scabra* at 0° and 45° angles, and for *C. digitalis* at 0° and 90° angles. Larger animals have a lesser % weight loss than smaller animals at these angles. There is no significant correlation between % weight loss after 5 hours and size for *C. scabra* on 90° angles and *C. digitalis* on 45° angles, over the size range tested. Pooling angles for the 2 species tested results in a significant correlation between % weight loss after 5 hours and length.

Field measurements show that average length of *Collisella scabra* declines linearly with angle. Large limpets would be expected on horizontal and intermediate sloped surfaces in the field if large animals experience less desic-

cation than small ones on these slopes. However, laboratory experiments suggest that there is not a significant difference in % water loss between large and small *C. scabra* on 90° angle surfaces. Small limpets do not lose less water than large ones on 90° surfaces. Thus the presence of small *C. scabra* on vertical surfaces in the field may not be explained by desiccation alone.

There is no significant relationship between length of *Collisella digitalis* and angle of substrate in the field. Laboratory experiments show that large *C. digitalis* lose less water than small ones on horizontal and vertical surfaces only. Large limpets would be expected on horizontal and vertical surfaces in the field if large animals experience less desiccation than small ones on these slopes. This does not explain the presence of large *C. digitalis* on intermediate sloped surfaces in the field.

It is concluded that the results of laboratory desiccation experiments do not alone explain the size distribution and abundance relationships found between the 2 species in the field. Differences in microalgal food selection between *Collisella digitalis* and *C. scabra* on different angles of substrate were investigated as an explanation for field observation (manuscript in preparation).

### Table 2

Summary of statistical analysis of regressions showing the relationship between percentage weight loss after 5 hours and length of limpet for *Collisella digitalis* and *Collisella scabra* at 3 different angles, and all angles combined.

| Species and angle | Regression Equation | r | df | p |
|---|---|---|---|---|
| *C. Scabra* | | | | |
| 0 | Y = 0.221 + −0.008x | −0.42 | 18 | < 0.05[5] |
| 45 | Y = 0.164 + −0.006x | −0.45 | 18 | .05 > p > .01[3] |
| 90 | Y = 0.108 + −0.001x | −0.07 | 18 | > .05 ns |
| *C. digitalis* | | | | |
| 0 | Y = 0.231 + −0.010x | −0.76 | 18 | < .01[4] |
| 45 | Y = 0.162 + −0.006x | −0.33 | 18 | > .05 ns |
| 90 | Y = 0.191 + −0.008x | −0.50 | 18 | .05 > p > .01[3] |
| All angles combined | | | | |
| *C. scabra* | Y = 0.274 + −0.014x | −0.62 | 58 | < .01[4] |
| All angles combined | | | | |
| *C. digitalis* | Y = 0.203 + −0.008x | −0.58 | 58 | < .01[4] |

[3] 0.05 > p > 0.01 significant
[4] p < 0.01 highly significant
ns not significant
[5] <0.05 significant

### DISCUSSION

HAVEN (1971) assumed, but did not test the hypothesis, that limpets on horizontal or gently sloping surfaces experience greater desiccation than on vertical or overhanging rocks because solar radiation hits horizontal rocks at a steeper angle of incidence and is therefore more intense per unit area. A number of factors can affect dehydration in limpets, including temperature, air movement, duration of drying (WOLCOTT, 1973), salinity dehydration (SEGAL & DEHNEL, 1962), geological nature of the rock upon which the limpet sits (DAVIES, 1970), limpet size (ABE, 1931; SHOTWELL, 1950; SEGAL, 1956; WOLCOTT, *op. cit.*), shape (RUSSELL, 1907; ORTON, 1929, 1933; WAGGE, 1952; MOORE, 1934; HATTAN, 1938; DAVIES, 1969) and species (WOLCOTT, *op. cit.*). Wolcott hypothesizes that the mucous sheet made by limpets, not size or surface-volume relationships, is the most important adaptation to desiccation. In my study it was observed that both *Collisella digitalis* and *C. scabra* made mucous sheets.

The role of desiccation in limiting distributions of organisms in the rocky intertidal zone has yet to be demonstrated. WOLCOTT (1973), NORTH (1954) and BOYLE (1970) suggest high mortality due to desiccation in smaller size classes. BREEN (1972) postulates that predation is the important factor in limiting distribution of small limpets.

Due to the many factors discussed above, it is not surprising that no clear relation between desiccation resistance and distributions of sympatric limpet species have been uncovered. To add to this is the probable technical impossibility of performing suitable experiments involving manipulation of all the factors such that their relative contributions to desiccation of limpets can be detected, using appropriate factorial statistical design and analysis.

In my experiments it was found that although no differences in desiccation resistance could be detected in a simple 3-way factorial experiment, there was evidence that small limpets of both species lose more water than do larger ones and this varies between the species depending on angle. However, the angles at which the smaller limpets were affected did not correlate with the observed limpet abundance ratio and angle trends in the field. Indeed, *Collisella scabra* tends to be larger at lower angles, but *C. digitalis* shows no such trends. Although resistance to desiccation may play a part in accounting for this distribution, especially in the upper intertidal ranges, it is clear that other factors may also be important. One of the least studied aspects of limpet competition is food resource allocation. It is likely that if rock angle affects the amount

of incident light hitting the substrate, this could have significant effects on the species composition and growth rates of the microalgae upon which the limpets feed. For example, the microhabitat differences of 5 sympatric species of Australian abalones have clearly been related to macroscopic algal distributions within their habitats (SHEPHERD, 1973).

The abundances of these limpets and their relation to substrate angle need to be studied from the point of view of competitive interactions with respect to food resource partitioning. Limpet abundance and size appear to be related to the availability of microalgae on a particular slope of substrate (MS in prep.). In the light of previous studies and the lack of a clearcut relation of substrate angle, species abundances and desiccation results, the food resource partitioning hypothesis is the more promising one to pursue in more detail. This is all the more likely to yield interesting and more controllable experiments in view of the fact that generally these species seem to have tolerances to desiccation greatly exceeding environmental stress conditions.

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